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CONTRIBUTIONS TO LIFE HISTORIES OF PLANTS, NO XI.

BY THOMAS MEEHAN.

On the Morphology of Bractless Inflorescence.

In various papers I have given illustrations to demonstrate that the variety of inflorescence known as extra-axillary results from the sudden arrestation of a growing shoot, and the immediate growth of the axillary bud, which pushes aside to a lateral position the former leader and effectually takes its place, only to be itself pushed aside by another developing axillary bud, when the proper time for that development has arrived.

Although this explanation is fully satisfactory so far as bracteated inflorescence is concerned, it does not explain the morphology of the naked flowered class, the exact nature of which has never been determined, and which, hitherto, I have never been able to understand.

One has only to read the chapter on "Inflorescence" in "Sach's Text Book" (English edition, p. 519 and following) to learn how confused and unphilosophical are prevailing notions concerning the nature of the various forms of inflorescence. That "Boraginaceæ and Solanaceæ" present an inflorescence determined by "the repeated dichotomy of an axillary bud," is better expressed by my proposition that it is determined by "the assumption of leadership by the axillary growth;" but though it is clear to Sachs that "the ultimate floral axes or pedicels of the flowers" are "not axillary in Aroideæ, Cruciferæ, &c.," he still insists "that every inflorescence originates from the normal terminal branching of a growing axis." "If bracts are conspicuously developed, the lateral axes arise in their axils; if they are inconspicuous or abortive, the lateral axes of the inflorescence are not axillary, but their mode of branching and growth remain the same as if the bracts were present." Though long satisfied that this diagnosis of naked inflorescence was wrong, and that there never had been theoretical bracts to abort, I have not, until now, been able to perceive that inflorescence is not all constructed on one plan; and that naked inflorescence, in particular, does not need the theoretical conception of bracts and axillary buds to account for its character.

In Saxifragaceæ most species are characterized by bracteated inflorescence, but there is a small section, of which *Saxifraga crassifolia* is the type, which has naked cymes. With one species of this section before me, *S. cordata,* it was evident that so wide a departure from the rest of its family could not be explained by any conception of axillary branching, such as a bracteated character involves. Abortion of the bracts could not by any possibility, have occurred. Neither could my own proposition of the pushing aside of a terminal axis by the growth of an axillary bud have any place in this arrangement. After many days of observation, thought, and comparison, the manner in which the inflorescence was formed became so clear, that the only surprise was that it had taken so many years to discover it.

The inflorescence of these Saxifrages is formed simply by *the elongation of the petioles and coalition of the stipules; the branchlets and the flowers, with their pedicels, are modifications of the leaf-blade; the veins forming the pedicels, and the flowers proceeding from buds formed at the apex of these veins.*

It is not necessary to go into close details, as the suggestion once given, any one with one or several plants before him can see that this is the fact. The bud scale, enclosing the embryonic flower scape is the enlarged and dilated base of a leaf, which, at the end of the past growing season, developed so far only as to form this scale. When the growing season arrives, this scale is rejuvenated, and increases a little in size, but the next one to elongate is perhaps double the length, with no increase in width. The next is still longer and narrower, with an imperfect leaf blade just beneath the apex. The perfect leaf blade at length ensues, with a still greater elongation of the dilated base, which we might now almost call the stipular portion. The next following has an inch, or sometimes more, of a petiole between the apex of this stipular portion and the leaf blade, still, however, with the apex of what would have been a bud-scale, apparent. It is important to note this projection as furnishing the key to what follows. The flower stem now pushes up, wholly leafless, but as the lower branchlet of the cymose inflorescence develops, we see the *apex before noted* in the axis, and by further observation may trace on one side of the main stalk, a ridge evidently formed by the overlapping outer edge of the coiled stipule. Succeeding branchlets show, but in a less degree, the same arrangement. The numerical order of the secondary branchlets of the inflorescence, and their general divergence and arrangement, correspond well with the main branchlets of the veins in the leaves, leaving no doubt in the mind of the thoughtful observer of their morphological identity.

Taking a glance at what occurs in other plants there is analogy for the view here taken. Some Begonias form leaf-buds at the end of their leading veinlets, as do many ferns; and a well known plant in cultivation, *Bryophyllum calycinum*, is increased mainly by such buds. Morphologically there is no difference between a leaf-bud and a flower-bud, so that we may reasonably expect flowers to appear where leaf-buds may exist. And in other respects *Bryophyllum* fortifies the position assumed for the Saxifrage. The leaves appearing at an early stage of growth are entire, and formed much as we find them in *Saxifraga cordata* but as the flowering stem progresses towards the flowering stage, the newer leaves become divided, and trifoliate—that is to say, the veins are comparatively destitute of their normal cellular covering, and are on their way to become the pedicels we find in the inflorescence of the Saxifrage.

I may conclude by reaffirming the proposition already presented, that nature does not depend on one method only as a plan for the formation of inflorescence; that in *Saxifraga cordata*, and probably in bractless inflorescence generally, the elongation and coiling of stipules or the dilated bases of leaf-stalks form the main axis or stem; and the leaf-blade the branches, branchlets and flowers.

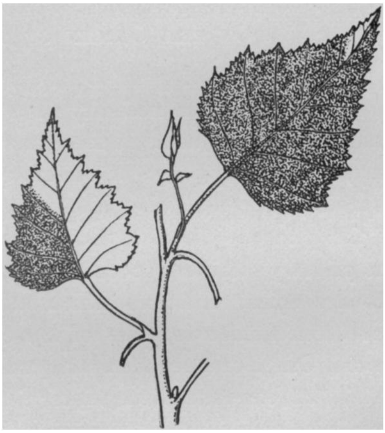
On Purple-Leaved Plants.

A large number of plants occasionally produce individuals with reddish or purple leaves. These are propagated by nurserymen, and are known in gardens as "blood-leaved" trees and shrubs. Thus we have blood-leaved oak, sycamore, beech, barberry and many others. Perpetuated by grafting, these retain the blood-leaved character through life, no variation from this characteristic having been placed on record.

No attempt to explain this eccentricity seems to have been made. It is well to place together facts that may ultimately lead to an explanation.

In flower paintings the leaves and vegetative parts of plants are usually represented of a uniform tint of green, but the real artist will tell us that there is seldom lacking a shade of brown or purple in some portions of leaves and branches that are in the highest conditions of vigor. The stronger growing shoots of the well-known *Pyrus japonica* are always of a bright rosy brown, only in those shoots growing in the interior of the plant, in partial shade, is the brown tint wanting. In the blood-leaved beech, the interior half-starved leaves have little of the brown, and the more vigorous the exposed branches are, the deeper is the shade. Blood-leaved trees themselves are, on the whole, more vigorous than the normal green-leaved forms from which, in the language of the nurseryman, they originally "sported." There is little doubt that in some unknown way, a vigorous vital power is accountable for the blood-leaved character in these cases.

A remarkable variation in the blood-leaved form of the common white birch has recently occurred. Some twelve years ago, a small plant was received from France. Some half a dozen were raised from it by grafting on a closely allied species, *Betula populifolia*. From the ends of some of the lowermost branches in two of these trees branchlets with the ordinary foliage of *Betula alba* have appeared. The dark "red" or purplish brown color of the leaves pervades the bark as well. In the reversion instanced not only the leaves but the branches have assumed the normal green. It is interesting to note that the reversion is not completed at once. The dark color first seems wanting in limited portions of the bark as the growth proceeds. At times the green part widens, then again lessens in length and width. In one case the dark portion extends as a hair line for four inches upwardly before it finally disappears. In one case half the leaf is purple, the other half green. There is no gradual shading off of the green and the brown,



but the lines are distinctly drawn where one tint ends and the other begins.

When these plants were grafted originally, one of the grafts one year old was broken completely off. The stock pushed out a branch of the blood-leaved form at a considerable distance down from the point at which the graft had been inserted, a note of which was made at the time in the "Botanical Gazette." This branch was of the same species as the parent, *Betula alba*, and not *Betula populifolia*, the stock.

We may conclude from these observations, that whatever the law may be which induces this change of color from the normal green to the blood-leaved condition, the change is effected in an original single cell or nucleus of the seed, and that the subsequent cells carry along the peculiarity of the mother cell through the whole life of the tree. It is further evident that it is an additional character, and not a change, as when the cell parts with it, as in the case of the birch cited, growth goes on just as before. In the case of the branch coming out below the point of union with the stock, we learn that the reproduction of daughter cells from a mother cell can take place downwardly as well as in other directions, and that *buds and branches can be produced from an original cell.* There is no distinction in nature between an axis and a leaf. They can both originate when the conditions favor, from a single cell, in any part of the plant.

ON THE ORIGIN OF THE APICAL CELL.

When treating of plant-tissues much has been said of the *punctum vegetationis*, and the necessity of a pre-existing *apical cell* before a branch can be formed. It does not seem to be conceded that any cell may, in an early stage of existence, produce a separate apical cell, capable of becoming the parent of a branch, whenever the exigencies of the plant require it. But I have had abundant evidence that the primary meristem or cambium tissue can, in emergencies, easily produce apical cells from which buds and branches can proceed. I have seen numerous cases of horse chestnuts, *Æsculus Hippocastanum*, Osage orange, *Maclura aurantiaca*, and Cottonwood, *Populus monilifera*, cut down in the winter time, that made buds and branches from the cambium tissue formed the preceding year, along the whole circumference of the tree stump. Hundreds of cells from this tissue would attempt to form shoots, many naturally being crowded out, but enough finally making a growth to present a miniature forest. The most remarkable case of this nature came under my observation in 1893, and relates to two large Carolina Cottonwoods, *Populus monilifera,* standing on the sidewalk at the corner of Greene and Harvey Streets, Germantown. About the time of the unfolding of the leaf, a horse had gnawed away the bark, exposing the wood for a space of nearly a foot in diameter. About midsummer, when the new cambium layer was being formed,[1] hundreds of buds developing to leaves and branches, appeared from the edge of the whole exposed surface of the new layer. It was a remarkable sight that a layer of tissue, usually content to cover a wound with new wood, should at the same time seem to be covered with scores of what one would call seedling trees if they had been at the surface of the earth.

It must be well known to observers of trees which have had large branches sawn off, that numerous buds producing branches will push through the bark of the stump near where the upper portion was cut away, proceeding, of course, from the primary meristem tissue which must have had the power to produce the necessary apical cells for this bud formation. But it is not often that the same power can be evidenced by similar growths from the exposed portions of wounds, as the observations here recorded afford.

The Fall of the Leaf in the Holly.

Near Philadelphia the spring growth of the American Holly, *Ilex opaca,* occurs in May. Simultaneously with the appearance of the new growth the ground is strewed with fallen leaves. I have thought, in common with most, if not all observers, that the swelling of the new growth dislodged the old leaves, just as it seems to do in the case of oak or beech leaves, where leaves that happen to remain dry on the branches all winter, drop when the new growth occurs in spring. To my surprise I find that this is not the case in the holly. After the copious fall already referred to, it is found that most of the fallen leaves were those of last year. Two-year-old leaves on the tree are abundant. Some of these are among the fallen ones, but few, apparently, in proportion to those from among the last season's growth. There is no fixed order in the dropping of the leaves. On a branch with say ten last year's leaves, it may be the first, fourth or fifth in the order of growth, or it may be a few of the later ones. In some cases all of the last year's growth will fall from the branch, leaving a few healthy leaves below of the year previous to the last. These will probably fall in a natural manner later in the season.

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[1] I have shown in the Proceedings of the Academy, 1866, pp. 292-293, that it is only about that time, in this tree, the tissue known as the cambium layer is formed.

Just here arises the question: What is the "natural manner" of the fall of the leaf? If a branch of any tree be broken off before maturity, the leaves dry, but remain attached to the parent branch. There is no "fall of the leaf" in this case. On the same branch, if it had been left on the parent stem, the leaf would have formed cork cells at the junction of petiole and stem, and have fallen by mere disarticulation at that point, in due season. Histology has taught us that cork cells are differentiated from other tissue, but the manner in which this has been brought about has not been demonstrated so far as the writer is aware. It has been thought that the following observations in connection with this subject may at least direct thought, if they throw little direct light on the subject.

On the leaves of the holly which are to fall, one or more small, black blotches underneath the epiderm appear here and there, being apparent both on the upper and under surface of these leaves. At this season the parenchyma takes on a yellow cast, the black blotches, however, retaining their character. Disarticulation then follows. The leaves which are perfectly green, and with no dark blotches on them, continue on the stem. The connection between these blotches and the fall of the leaf is undoubted, and we may almost as logically say they are connected with the formation of the cork cells which act directly in disarticulation.

Those of us who have had a wide experience with living vegetation have no difficulty in surmising that these dark blotches are of a fungous character. My good friend, the eminent mycologist, Mr. J. B. Ellis, of Newfield, New Jersey, after a microscopic examination of these fallen leaves, finds evidence that the marks are caused by a minute fungus, though in this and similar instances he has never been able to get nearer the fact than that they are manifestations of some zymotic organism that permeates the whole structure of the individual during its progressive growth.

I have, in other papers, shown that the bark of trees is not decorticated in any mechanical way, but by the growth of cork cells, each species having its own time and manner of development. In some trees these cells become active on bark but one or two years old, while in the chestnut, *Castanea*, and some others it may be twenty or more years before any sign of a "rough" bark appears, through the quiescence of the cork cells. No one, as I have already hinted, seems to have been able to demonstrate the causes which lead to these varying and remarkable results.

In the case of these holly leaves it is evident that they do not fall in response to the requirements of any definite period of maturity, but that the cork cells which provide for disarticulation are simultaneous with the destruction of the parenchyma. This is apparently the work of an adventitious agency, not essential to, but in some way co-ordinate with the regular economy of the plant.

ON BEES AND HONEY-SUCKLES.

I was interested to-day, June 18th, in noting that while a few honey bees persistently collected nectar from the mouths of honey-suckles, by far the larger number collected from the fallen flowers only.

The plant was *Lonicera japonica*, in the two forms known in gardens as *L. brachypoda*, and *L. flexuosa*, both intertwining and flowering together. I have, in the past, satisfied myself that a bee which starts from the hive for pollen pays no attention to gathering nectar, while the one looking for nectar collects that only. Whether this is the course of labor for that trip from the hive only,or whether these particular tasks occupy the whole day or more, may be an interesting question. I had never noted bees collecting nectar from fallen flowers; indeed had not noted that fallen flowers had nectar, so that the attention of the bees to them gave the subject a double interest.

The flowers are white when freshly opened, the next day yellowish, the following they wither slightly and fall. Large numbers are collected by the leaves on which they mostly lie till they turn brown and shrivel completely. Those which were badly shrivelled seemed preferable to the bees.

On cutting across the tube of a white corolla near the base, and then gently stripping the flower downwardly a large globule of nectar protrudes. The same process executed on the older or yellow flower, gives about the same quantity as also does the faded flower of the third day. In the dried flower, taken before much shrivelling had occurred, nearly as much nectar was found. The completely shrivelled and twisted flower could not be "stripped" of its secretion in this way, but it was certainly present and as abundant. The bees carefully sought what would have been the mouth of the corolla, and then extracted the sweets from that point. It soon became evident that the shrivelling and contracting of the tube of the corolla acted in the same manner as the thumb-nail and finger in "stripping," lessening the diameter of the tube, and forcing the nectar towards the mouth, and within the reach of the visiting insect.

As noted, the bees collecting nectar from these dead flowers, never visited the fresh opening ones; while the few visiting the fresh flowers never visited the dead or dying ones; a very careful watch of half an hour satisfied me on this point. It was noted that the latter took considerable time and much labored effort with each flower. There was an average of fifteen seconds to each flower, a very long time for the average honey-making bee. Those working on the drying flowers made no more than the ordinary effort of bees with fresh flowers. It was difficult to understand why in the same variety of insect should each have its own line of procedure. If it should be suggested that bees could profit by experience, and that those which confined themselves to the freshly opened flowers were young bees that had yet much to learn, there still remains the fact that they did not profit by the experience of the older bees. Sometimes almost side by side, it might be supposed that any creature that could profit by experience, would want to know what the one picking at a dried flower had found.

The relation between insects and flowers obtrudes itself here. Many plants, as I have placed on record, shed their pollen and cover the stigma before the opening of the corolla. Whether the stigma is in receptive condition or not, the pollen remains there till it is, and we may regard all such as "arranged for self-fertilization," if, indeed, there is any such special arrangement in the vegetable world wholly with this view, or with the special view of cross-fertilization. But in this honey-suckle the anther sacs burst immediately on expansion and the anthers are in such close position to the stigma that it can scarcely do aught but receive its own-pollen. All the flowers examined seemed to have the stigmas completely covered with pollen, and I feel pretty sure, with own-pollen. My plants are, however, infertile, rarely a few berries mature. I should refer this to propagation from an infertile plant, as we frequently find to occur in all classes of ligneous plants, which fruit neither with own-pollen nor foreign pollen, rather than to any want of ability in own-pollen to produce fertilization as an abstract principle, as would be assumed by some.

There still remains to be discussed why all this large amount of nectar should be secreted by the flower with no apparent benefit to itself in any conceivable way. But it is not safe to say, that, because we can not see that any benefit results in relation to the visits of insects, it is of no value in some, as yet, undiscovered operation in the economy of nature. For aught we know it may be an excretion rather than a secretion, which it may be as much an advantage to get rid of when of no further use to the plant, as it is an advantage to get rid of the corolla itself.

A very curious circumstance in connection with these observations was the discovery that each of these two forms of the *Lonicera japonica,* have different times of the day for the opening of its blossoms. The expansion, as in so many points of growth, is rhythmic and not a continuous effort. In the form known as *Lonicera flexuosa,* the lobes of the corolla parted so as to admit of the protrusion of the stamens at 2 P. M. Further efforts at expansion rested till 4 P. M., when the act was resumed and completed. *L. brachypoda* commenced opening at 5 P. M., and completed the opening by 7 P. M.

There is no reason why variation may not occur in the behaviour of plants as well as in the parts of their structure, but it is difficult to conceive of any physiological value in these variations from any point of view in the economy of plant life.